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Morphology, genetic characterization and mitochondrial genome of *Gorgorhynchus fistularius* sp. nov. (Acanthocephala, Isthmosacanthidae) from the red cornetfish *Fistularia petimba* (Lacépède, 1803) (Gasterosteiformes, Fistulariidae), with phylomitogenomics of the family Isthmosacanthidae

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Abstract

The family Isthmosacanthidae is a group of acanthocephalans mainly parasitic in fishes of Osteichthyes. A new isthmosacanthid species, *Gorgorhynchus fistularius* **sp. nov.** (Polymorphida, Isthmosacanthidae) is described based on specimens collected from the red cornetfish *Fistularia petimba* (Lacépède, 1803) (Syngnathiformes, Fistularidae) using the integrated morphological characters and molecular data. The complete mitochondrial genome of *G. fistularius* **sp. nov.** is presented, which is 14,409 bp in length and represents the first mitogenomic data for the genus *Gorgorhynchus* and also for the family Isthmosacanthidae. Comparative mitogenomic analysis revealed that the overall A+T content (68.1%) in the mitogenome of *G. fistularius* **sp. nov.** is distinctly higher than that of the other mitogenomes of the order Polymorphida reported so far (54.5–64.4%), but the composition and gene rearrangement of the mitogenome of *G. fistularius* **sp. nov.** are identical to the current known mitogenomes of polymorphid species except for *Southwellina hispida*. Mitogenomic phylogenies supported the Isthmosacanthidae as a distinct family, and suggested new insights into the interfamilial relationships occurring as Plagiorhynchidae + [Isthmosacanthidae + (Centrorhynchidae + Polymorphidae)] in the order Polymorphida.

Key Words

Acanthocephala, Polymorphida, integrative taxonomy, mitochondrial genome, red cornetfish, phylogeny

Introduction

The phylum Acanthocephala is among the commonest groups of zooparasites, with over 1,300 described species occurring in the alimentary canal of all major vertebrate groups (Petrochenko 1956; Yamaguti 1963; Nickol 1985; Amin 2013; Perrot-Minnot et al. 2023). According to the current classifications, Acanthocephala includes approximately 150 genera and 30 families assigned into 10 orders (Amin 2013). Recently, some molecular phylogenies using different genetic markers, especially mitochondrial genomes, solved the phylogenetic relationships of some certain taxa, and also substantially improved and challenged the current classifications of Acanthocephala (Steinauer et al. 2005; Weber et al. 2013; Gazi et al. 2016; García-Varela and Andrade-Gómez 2021; Huston and Smales 2020; Muhammad et al. 2020a, 2020b, 2020c; Zhao et al. 2023, 2024, 2025; Li et al. 2024; Xie et al. 2024, 2025a, 2025b). However, due to the scarcity and inaccessibility of genetic data for many family or

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order-level taxa, our current knowledge of the molecular phylogenetic framework of the Acanthocephala is still far from comprehensive.

The family Isthmosacanthidae (type genus *Isthmosacanthus*) was established by Smales (2012), who originally placed this family into the order Echinorhynchida, and transferred the genera *Golvanorhynchus* and *Gorgorhynchoides* into the Isthmosacanthidae. However, Amin (2013) rejected the assignment of *Gorgorhynchoides* and *Golvanorhynchus* into the Isthmosacanthidae, but accepted the validity of this family. The recent phylogenetic studies based on a single (18S / 28S / *cox*1) or some concatenated genetic markers (18S + 28S / 18S + 28S + *cox*1) supported that the Isthmosacanthidae belongs to the order Polymorphida, and proposed to transfer the genera *Metarhadinorhynchus* (now as synonym of *Gorgorhynchoides*), *Gorgorhynchus* and *Serrasentis* into the Isthmosacanthidae (Lisitsyna et al. 2019; Huston et al. 2020; Huston and Smales 2021; García-Varela and Andrade-Gómez 2021; Kita et al. 2024; García-Varela et al. 2024). Consequently, the Isthmosacanthidae currently contains five genera, namely *Isthmosacanthus*, *Golvanorhynchus*, *Gorgorhynchus*, *Metarhadinorhynchus* and *Serrasentis* (Smales 2012; Huston et al. 2020; García-Varela and Andrade-Gómez 2021; Kita et al. 2023, 2024; García-Varela et al. 2024). However, the phylogenetic relationships between the Isthmosacanthidae and the other families within Polymorphida remain unsolved.

The red cornetfish *Fistularia petimba* (Lacépède, 1803) (Syngnathiformes, Fistularidae) is mainly distributed in the tropical Atlantic and Indo-West Pacific Oceans, including the South and East China Sea, which mainly feeds on small fishes and shrimps (Froese and Pauly 2019; Cerim et al. 2021). To date, only two acanthocephalan species have been reported from this fish host, namely *Serrasentoides fistulariae* (Echinorhynchida, Rhadinorhynchidae) and *Australorhynchus tetramorphacanthus* (Echinorhynchida, Rhadinorhynchidae) (Parukhin 1971; Amin et al. 2019).

In the present study, some isthmosacanthid specimens were collected from the red cornetfish *F. petimba* in the South China Sea, which were identified to species level using morphological methods (light and scanning electron microscopy) and molecular techniques (sequencing and analyses of the nuclear small ribosomal subunit (18S), large ribosomal subunit (28S) and internal transcribed spacer (ITS), and the mitochondrial cytochrome c oxidase subunit I (*cox*1) and subunit II (*cox*2) genes. Moreover, the complete mitochondrial genome of this species, representing the first mitogenomic data for the family Isthmosacanthidae, was also sequenced and annotated to enrich the mitogenomes of Acanthocephala. In order to further evaluate the phylogenetic position of the Isthmosacanthidae, phylogenetic analyses based on the concatenated amino acid sequences of 12 protein-coding genes (PCGs) of mitochondrial genomes were performed using maximum likelihood (ML) and Bayesian inference (BI) methods, respectively.

Materials and methods

Morphological observation

Acanthocephalan specimens were isolated from the intestine of *F. petimba* from the South China Sea (off Sanya, Hainan Island, China). Specimens were washed and kept in cold water for several hours until the proboscis everted, and then stored in 80% ethanol until studied. For light microscopical studies, specimens were made in impermanent mount slide and cleared in lactophenol. Preparation of samples for SEM observation was according to the previous studies (Ru et al. 2022; Chen et al. 2024; Zhao et al. 2024; Wang et al. 2025).

Molecular procedures

Genomic DNA from the mid-body of 1 male and 2 female individuals was extracted using a Column Genomic DNA Isolation Kit (Shanghai Sangon, China) according to the manufacturer's instructions. The target regions of 18S, 28S, ITS, *cox*1 and *cox*2 were amplified using the primers under cycling conditions provided in Table 1. PCR products were purified and sequenced according to the previous studies (Li et al. 2019; Chen et al. 2024; Wang et al. 2025). The DNA sequences obtained herein were compared (using the algorithm BLASTn) with those available in the National Center for Biotechnology Information (NCBI) database (http://www.ncbi.nlm.nih.gov).

Mitochondrial genome sequencing, assembly and annotation

A total of 50 GB of clean data were generated using the Pair-End 150 sequencing method on the Illumina NovaSeq 6000 platform by Novogene (Tianjin, China). The protocol and procedure for assembly and annotation of the complete mitochondrial genomes of the present material are according to the previous studies (Zhao et al. 2023; Xie et al. 2024; Li et al. 2024). The complete mitochondrial genome of present material obtained herein has been deposited in the GenBank database (http://www.ncbi.nlm.nih.gov, under the accession number PX769935).

Phylogenetic analyses

Phylogenetic analyses of Acanthocephala were conducted based on the concatenated amino acid (AA) sequences of the 12 PCGs of mitogenomes using maximum likelihood (ML) and Bayesian inference (BI) methods, respectively. *Rotaria rotatoria* and *Philodina citrina* (Rotifera, Bdelloidea) were chosen as the out-group. The in-group included the present material and the other 47 acanthocephalan species. Detailed information on the representatives of Acanthocephala included in the present phylogeny is

Table 1. The primers and cycling conditions for amplifying different target regions by polymerase chain reaction (PCR) in the present study.

Primer	Sequence 5'-3'	Cycling condition	Reference
18S	18S-F: 5'-AGATTAAGCCATGCATGCGTAAG-3'	95 °C for 2 min	Garey et al. (1996)
		95 °C for 30 s	
	18S-R: 5'-TGATCCTTCTGCAGGTTCACCTAC-3'	55 °C for 30 s	
		72 °C for 90 s (35 cycles)	
		72 °C for 5 min	
28S	28S-1-F: 5'-CAAGTACCGTGAGGGAAAGTTGC-3'	94 °C for 3 min	García-Varela and Nadler (2005)
	28S-1-R: 5'-CAGCTATCCTGAGGGAAAC-3'	94 °C for 1 min	
	28S-2-F: 5'-ACCCGAAAGATGGTGAACTATG-3'	55 °C for 1 min	
	28S-2-R: 5'-CTTCTCCAAC(T/G)TCAGTCTTCAA-3'	72 °C for 1 min (35 cycles)	
	28S-3-F: 5'-CTAAGGAGTGTGTAACAACTCACC-3'	72 °C for 7 min	
	28S-3-R: 5'-AATGACGAGGCATTTGGCTACCTT-3'		
	28S-4-F: 5'-GATCCGTAACTTCGGGAAAAGGAT-3'		
	28S-4-R: 5'-CTTCGCAATGATAGGAAGAGCC-3'		
ITS	ITS-F: 5'-GTCGTAACAAGGTTTCCGTA-3'	94 °C for 2 min	Král'ová-Hromadová et al. (2003)
		94 °C for 20 s	
	ITS-R: 5'-TATGCTTAAATTCAGCGGGT-3'	51 °C for 20 s	
		65 °C for 50 s (40 cycles)	
		65 °C for 5 min	
cox1	*cox*1-F: 5'-GGTCAACAAATCATAAAGATATTGG-3'	94 °C for 1 min	Gómez et al. (2002)
		94 °C for 1 min	
	*cox*1-R: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	45 °C for 30 s	
		72 °C for 1 min (35 cycles)	
		72 °C for 10 min	
cox2	*cox*2-F: 5'-AATGTTTGATGGGTTTAGAG-3'	94 °C for 3 min	Present study
		94 °C for 30 s	
	*cox*2-R: 5'-AACACTGACCATATATAACC-3'	45 °C for 30 s	
		72 °C for 1 min (33 cycles)	
		72 °C for 10 min	

provided in Table 2. The extracted amino acid sequences were aligned separately using MAFFT v7.313 under the iterative refinement method of E-INS-I (Katoh and Standley 2013). The aligned AAs sequences were concatenated into a single alignment matrix by PhyloSuite v1.2.2 (Zhang et al. 2020). For Bayesian inference, the JTT+F+I+G4 model was identified as the best-fit substitution model according to the Bayesian Information Criterion (BIC) using ModelFinder (Kalyaanamoorthy et al. 2017). Bayesian inference was run using MrBayes v3.2 for 5×10^6 MCMC generations. The maximum likelihood (ML) inference was performed using IQTREE v2.1.2 under the parameters kept at default (Golombek et al. 2015; Minh et al. 2020). The mtInv+F+I+G4 model was identified as the best-fit substitution model according to the Akaike Information Criterion (AIC) using ModelFinder for ML inference. Node support in ML inference was evaluated using 1000 bootstrap (BS) replicates.

Data availability

The nuclear and mitochondrial DNA sequences of *G. fistularius* sp. nov. obtained herein were deposited in the GenBank database [http://www.ncbi.nlm.nih.gov, accession numbers: PX753218–PX753220 (18S); PX753221–PX753223 (28S); PX758632–PX758634 (ITS); PX753371–PX753373 (*cox*1); PX754246–PX754248 (*cox*2); PX769935 (mitogenomic)]. Type specimens of *G. fistularius* sp. nov. (HBNU-A-F20241217-1CL, HBNU-A-F20241217-2CL) were deposited in the College of Life Sciences, Hebei Normal University, Hebei Province, China.

Results

Morphology of *Gorgorhynchus fistularius* sp. nov.

Family Isthmosacanthidae Smales, 2012
Genus *Gorgorhynchus* Chandler, 1934

***Gorgorhynchus fistularius* sp. nov.**

https://zoobank.org/0A73F76B-8E27-4B9C-8D78-0EFC4DE52A13

Figs 1–3, Table 3

Type-host. Red cornetfish *Fistularia petimba* (Lacépède, 1803) (Gasterosteiformes, Fistulariidae).

Type-locality. South China Sea (off Sanya, Hainan Island, China).

Site in host. Intestine.

Table 2. Detailed information of representatives with their mitogenomic data included in the present phylogeny.

Taxon	Order	Family	Species	Accession	Length	AT%	Reference
Out-group							
Rotifera							
Eurotatoria	Bdelloidea	Philodinidae	*Rotaria rotatoria*	NC_013568	15319	73.2	Min and Park (2009)
			Philodina citrina	FR856884	14003	77.7	Weber et al. (2013)
In-group							
Acanthocephala							
Archiacanthocephala	Moniliformida	Moniliformidae	*Moniliformis* sp.	OK415026	14066	66.2	Dai et al. (2022)
			Moniliformis tupaia	OP413683	14150	63.8	Unpublished
	Oligacanthorhynchida	Oligacanthorhynchidae	*Macracanthorhynchus hirudinaceus*	NC_019808	14282	65.2	Weber et al. (2013)
			Oncicola luehei	NC_016754	14281	60.2	Gazi et al. (2012)
Eoacanthocephala	Gyracanthocephala	Quadrigyridae	*Acanthogyrus bilaspurensis*	MT476589	13360	59.3	Unpublished
			Acanthogyrus cheni	KX108947	13695	65.3	Song et al. (2016)
			Pallisentis celatus	NC_022921	13855	61.5	Pan and Nie (2013)
	Neoechinorhynchida	Neoechinorhynchidae	*Neoechinorhynchus violentum*	KC415004	13393	59.4	Pan and Jiang (2018)
			Neoechinorhynchus qinghaiensis	MW851291	13271	65.8	Unpublished
			Neoechinorhynchus sp. (*Acanthocephalus* sp.)	MT345686	13269	65.1	Unpublished
		Tenuisentidae	*Paratenuisentis ambiguus*	NC_019807	13574	66.9	Weber et al. (2013)
Palaeacanthocephala	Echinorhynchida	Arhythmacanthidae	*Heterosentis pseudobagri*	OP278658	13742	62.5	Gao et al. (2023)
		Cavisomidae	*Cavisoma magnum*	MN562586	13594	63.0	Muhammad et al. (2020a)
		Echinorhynchidae	*Echinorhynchus truttae*	NC_019805	13659	63.1	Weber et al. (2013)
		Heteracanthocephalidae	*Aspersentis megarhynchus*	PP965112	14661	64.6	Xie et al. (2024)
		Leptorhynchoididae	*Brentisentis yangtzensis*	MK651258	13864	68.3	Song et al. (2019)
			Leptorhynchoides thecatus	NC_006892	13888	71.4	Steinauer et al. (2005)
		Micracanthorhynchinidae	*Micracanthorhynchina dakusuiensis*	OP131911	16309	56.8	Gao et al. (2022)
			Micracanthorhynchina hemirhamphi	PV590120	17272	60.5	Xie et al. (2025b)
		Pomphorhynchidae	*Longicollum pagrosomi*	PV053864	14596	55.8	Zhao et al. (2025)
			Longicollum sp.	OR215045	14632	55.8	Unpublished
			Pomphorhynchus bulbocolli	JQ824371	13915	59.9	Unpublished
			Pomphorhynchus laevis	MN562482	13881	57.5	Unpublished
			Pomphorhynchus rocci	JQ824373	13845	60.7	Unpublished
			Pomphorhynchus tereticollis	JQ809452	13890	56.8	Unpublished
			Pomphorhynchus zhoushanensis	PV053863	14444	55.7	Zhao et al. (2025)
		Pseudoacanthocephalidae	*Pseudoacanthocephalus bufonis*	MZ958236	14056	58.4	Zhao et al. (2023)
			Pseudoacanthocephalus sp.	OQ588705	14883	61.5	Unpublished
			Pseudoacanthocephalus sichuanensis	PP476191	15812	56.8	Zhao et al. (2024)
			Pseudoacanthocephalus nguyenthileae	PP476192	13701	56.3	Zhao et al. (2024)
		Rhadinorhynchidae	*Rhadinorhynchus laterospinosus*	PV590110	13567	62.9	Xie et al. (2025b)
	Polymorphida	Centrorhynchidae	*Centrorhynchus aluconis*	KT592357	15144	54.5	Gazi et al. (2016)
			Centrorhynchus clitorideus	MT113355	15884	55.5	Muhammad et al. (2020c)
			Centrorhynchus milvus	MK922344	14314	54.5	Muhammad et al. (2019a)
			Sphaerirostris lanceoides	MT476588	13478	58.0	Muhammad et al. (2020b)
			Sphaerirostris picae	MK471355	15170	58.1	Muhammad et al. (2019b)
		Isthmosacanthidae	*Gorgorhynchus fistularius* sp. nov.	PX769935	14409	68.1	Present study

Taxon	Order	Family	Species	Accession	Length	AT%	Reference
		Plagiorhynchidae	*Plagiorhynchus transversus*	NC_029767	15477	61.1	Gazi et al. (2016)
		Polymorphidae	*Bolbosoma balaenae*	MZ357084	14301	62.6	García-Gallego et al. (2023)
			Bolbosoma capitatum	MZ357085	14319	63.9	García-Gallego et al. (2023)
			Bolbosoma nipponicum	OR468096	14296	60.9	Li et al. (2024)
			Bolbosoma vasculosum	MZ357087	14313	63.9	García-Gallego et al. (2023)
			Corynosoma bullosum	PQ516697	14879	63.8	Xie et al. (2025a)
			Corynosoma evae	PQ516696	13947	61.6	Xie et al. (2025a)
			Corynosoma villosum	OR468095	14241	61.0	Li et al. (2024)
			Polymorphus minutus	MN646175	14149	64.4	Sarwar et al. (2021)
			Southwellina hispida	NC_026516	14742	63.9	Gazi et al. (2015)
Polyacanthocephala	Polyacanthorhynchida	Polyacanthorhynchidae	*Polyacanthorhynchus caballeroi*	NC_029766	13956	56.3	Gazi et al. (2016)

Type specimens. Holotype, male (HBNU-A-F20241217-1CL); paratypes: 4 males, 4 females (HBNU-A-F20241217-2CL); deposited in the College of Life Sciences, Hebei Normal University, Hebei Province, China.

Etymology. The species name refers to the generic name of the type host.

Description. General. Trunk long and slender, nearly cylindrical; armed with single field of about 13–20 irregular and incomplete circles of small spines anteriorly; tightly packed circles of spines, spines distinctly becoming sparser and larger towards posteriorly (Figs 1A, 2A, 3A). Proboscis clavate, armed with 20–22 spiral longitudinal rows of 10–12 hooks each (Figs 1A–C, 2A, C, E, 3A, B); first 2–6 hooks of each from anteriorly with simple roots, hooks 1 usually small, hooks 2 and 3 largest, hooks 7–12 without roots, hooks 4–12 gradually decreasing in size; without dorso-ventral differentiation of hook and root sizes. Neck well developed, more or less cylindrical (Figs 1A, 2A, 3A). Proboscis receptacle double-walled, cerebral ganglion at base of proboscis receptacle (Figs 1A, 3A). Lemnisci very long, unequal, tubular, distinctly longer than proboscis receptacle (Figs 1A, 3A).

Male [Based on 5 mature specimens]. Trunk 46.0–65.5 (53.1) mm long, maximum width 570–800 (664). Proboscis 550–750 (646) long, 280–410 (346) wide. Proboscis hooks similar in shape, 38–52 (46), 58–70 (65), 63–73 (67), 61–72 (66), 60–69 (64), 57–63 (61), 55–61 (58), 48–57 (54), 46–55 (51), 33–48 (43), 29–45 (37) in length from anteriorly to posteriorly. Neck 300–350 (336) long, 290–390 (324) wide. Proboscis receptacle 1.50–1.92 (1.61) mm long, 250–370 (296) wide. Shorter lemniscus 3.90–5.20 (4.64) mm long, 70–150 (106) wide; longer lemniscus 4.70–5.80 (5.31) mm long, 110–130 (118) wide. Testes two, oval, nearly equal in size (Figs 1E, 3F); anterior testis 1.20–1.50 (1.32) mm long, 420–500 (458) wide; posterior testis 1.27–1.60 (1.38) mm long, 450–600 (510) wide. Cement glands four, very long, tubular, clustered together (Figs 1E, 3F); a short distance from posterior testis, shorter cement glands 5.98–16.6 (10.3) mm long, 122–195 (159) wide; longer cement glands 12.0–22.0 (16.0) mm long, 146–220 (177) wide. Saefftigen's pouch rod-shaped, 1.20–1.80 (1.43) mm long, 450–640 (505) wide (Figs 1E, 3D, F). Copulatory bursa not everted. Gonopore nearly terminal.

Female [Based on 4 mature specimens]. Trunk 55.3–110.5 (83.3) mm long, maximum width 650–1080 (913). Proboscis 650–800 (733) long, 370–480 (445) wide. Proboscis hooks similar in shape, 45–69 (63), 61–79 (70), 68–85 (75), 66–82 (74), 65–79 (72), 62–77 (71), 60–76 (68), 58–75 (68), 51–72 (65), 42–69 (60), 40–65 (57) in length from anteriorly to posteriorly. Neck 380–500 (428) long, 330–450 (368) wide. Proboscis receptacle 1.63–1.95 (1.82) mm long, 310–430 (378) wide. Shorter lemniscus 4.76–7.93 (6.27) mm long, 80–171 (130) wide; longer lemniscus 4.88–8.29 (6.86) mm long, 70–220 (146) wide. Uterine bell 570–900 (743) long, 170–300 (220) wide; uterus 500–620 (568) long, vagina 260–700 (428) long (Figs 1F, 3C). Eggs ellipsoid, 40–93 (63) × 20–50 (32) in size (n = 20) (Figs 1H, 2F, 3E). Gonopore subterminal.

Molecular characterization

Partial 18S region

Three partial 18S sequences of *G. fistularius* sp. nov. obtained herein are all 1661 bp in length, with no nucleotide divergence detected. In the genus *Gorgorhynchus*, only *G. medius* with 18S data (OR886454) is available in GenBank. Pairwise comparison of the 18S sequences of *G. fistularius* sp. nov. with that of *G. medius* showed 0.24% of nucleotide divergence. The 18S sequences of *G. fistularius* sp. nov. obtained herein were deposited in GenBank database (http://www.ncbi.nlm.nih.gov) (under accession numbers PX753218–PX753220).

Partial 28S region

Three partial 28S sequences of *G. fistularius* sp. nov. obtained herein are all 2819 bp in length, with no nucleotide divergence detected. In the genus *Gorgorhynchus*, only *G. medius* with 28S data (OR886457) is available in GenBank. Pairwise comparison of the 28S sequences

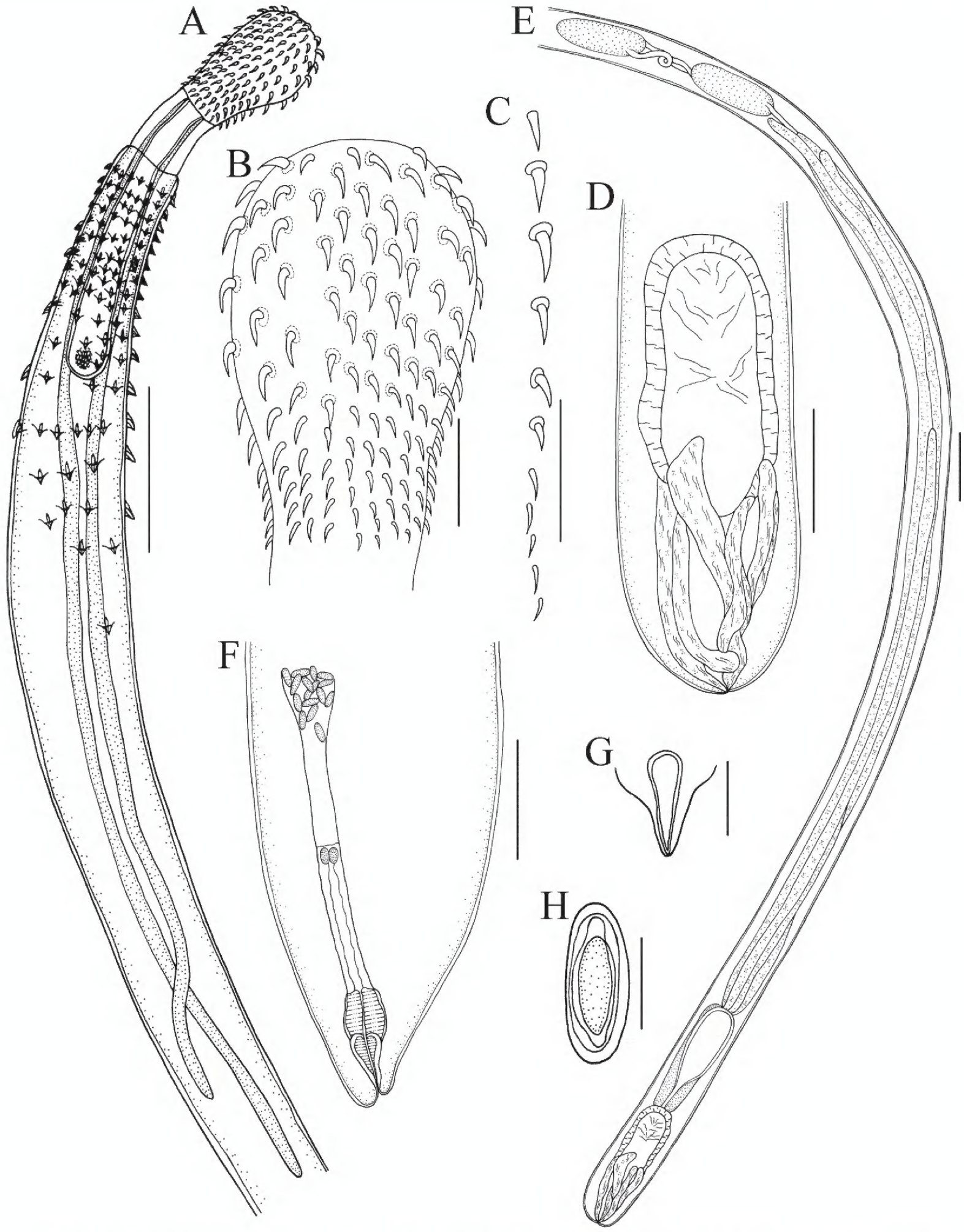

Figure 1. *Gorgorhynchus fistularius* sp. nov. collected from *Fistularia petimba* (Lacépède) (Gasterosteiformes, Fistulariidae) in China. **A.** Anterior part of female; **B.** Proboscis; **C.** Longitudinal row of hooks; **D.** Posterior end of male; **E.** Posterior part of male; **F.** Posterior end of female; **G.** Trunk spine; **H.** Egg. Scale bars: 1000 μm (**A, E**); 200 μm (**B, C**); 500 μm (**D, F**); 30 μm (**G, H**).

of *G. fistularius* sp. nov. with that of *G. medius* showed 1.04% of nucleotide divergence. The 28S sequences of *G. fistularius* sp. nov. obtained herein were deposited in GenBank database (http://www.ncbi.nlm.nih.gov) (under accession numbers PX753221–PX753223).

Partial ITS region

Three partial ITS sequences of *G. fistularius* sp. nov. obtained herein are all 851 bp in length, with no nucleotide divergence detected. There is no ITS data of *Gorgorhynchus* or isthmosacanthid species reported so far. The ITS sequences of *G. fistularius* sp. nov. obtained herein were deposited in GenBank database (http://www.ncbi.nlm.nih.gov) (under accession numbers PX758632–PX758634).

Partial *cox*1 region

Three partial *cox*1 sequences of *G. fistularius* sp. nov. obtained herein are all 655 bp in length, with no nucleotide divergence detected. There are three species of

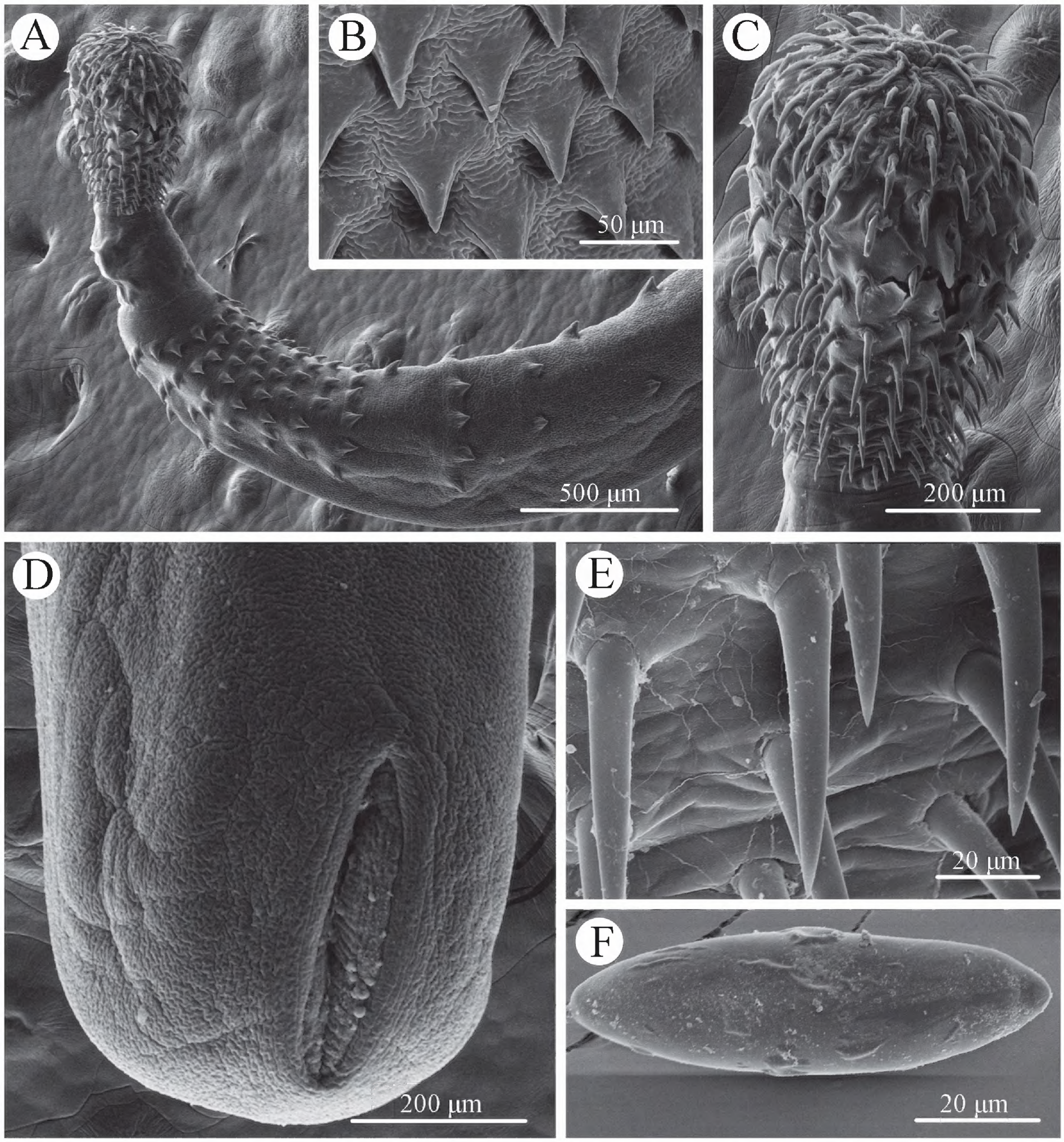

Figure 2. Scanning electron micrographs of *Gorgorhynchus fistularius* sp. nov. collected from *Fistularia petimba* (Lacépède) (Gasterosteiformes, Fistulariidae) in China. **A.** Anterior part of female; **B.** Magnified image of trunk spines; **C.** Proboscis of female; **D.** Posterior end of female; **E.** Magnified image of proboscis hook; **F.** Egg.

Gorgorhynchus with *cox*1 available in GenBank, including *G. medius* (OR883561, OR883562), *G. lepidus* (OR826976–OR826980) and *Gorgorhynchus* sp. (MK937568). Pairwise comparison of the *cox*1 sequences *G. fistularius* sp. nov. with that of *Gorgorhynchus* spp. available in GenBank, displayed 17.4% (*G. lepidus*, OR826977) to 18.0% (*G. lepidus*, OR826976) of nucleotide divergence. The *cox*1 sequences of *G. fistularius* sp. nov. obtained herein were deposited in GenBank database (http://www.ncbi.nlm.nih.gov) (under accession numbers PX753371–PX753373).

Partial *cox*2 region

Three partial *cox*2 sequences of *G. fistularius* sp. nov. obtained herein are all 318 bp in length, with no nucleotide divergence detected. There is no *cox*2 data of *Gorgorhynchus* or isthmosacanthid species reported so far. The *cox*2 sequences of *G. fistularius* sp. nov. obtained herein were deposited in GenBank database (http://www.ncbi.nlm.nih.gov) (under accession numbers PX754246–PX754248).

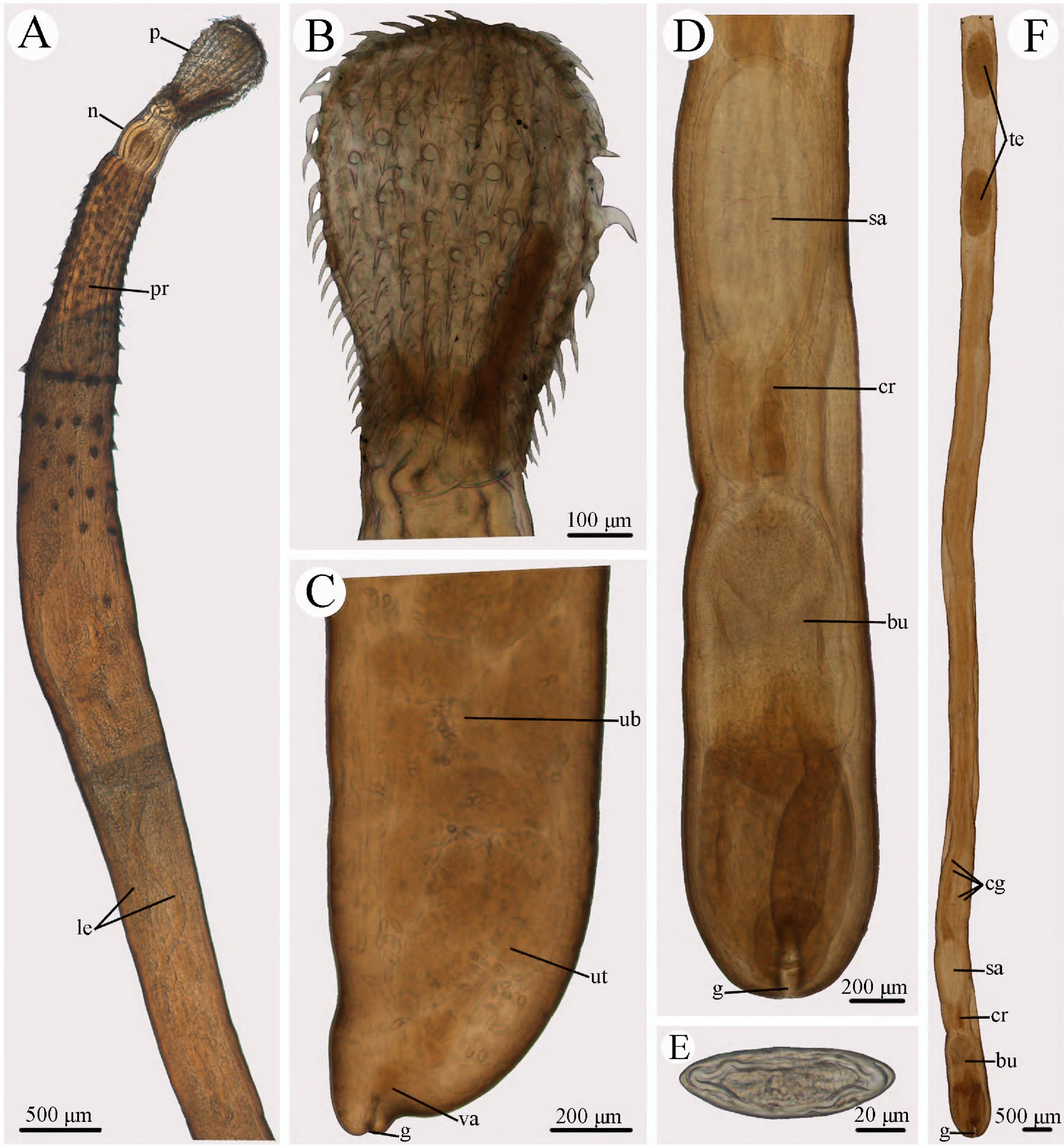

Figure 3. Photomicrographs of *Gorgorhynchus fistularius* sp. nov. collected from *Fistularia petimba* (Lacépède) (Gasterosteiformes, Fistulariidae) in China. **A.** Anterior part of male; **B.** Proboscis of male; **C.** Posterior part of female; **D.** Posterior part of male (copulatory bursa not everted); **E.** Egg; **F.** Posterior part of male. Abbreviations: bursa (**bu**); cement glands (**cg**); cement reservoir (**cr**); gonopore (**g**); lemniscs (**le**); neck (**n**); proboscis (**p**); proboscis receptacle (**pr**); saeftigen's pouch (**sa**); testis (**te**); uterine bell (**ub**); uterus (**ut**); vagina (**va**).

Remarks

The genus *Gorgorhynchus* currently includes 13 species mainly parasitic in marine fishes (Amin and Van Ha 2011; Amin 2013; Smales et al. 2019). In the genus *Gorgorhynchus*, the new species has the trunk spines arranged in a single anterior field, and proboscis with 20–22 longitudinal rows of 10–12 hooks each, which is similar to *G. clavatus* Van Cleave, 1940 and *G. lepidus* Van Cleave, 1940 (see Table 3 for details). *Gorgorhynchus fistularius* sp. nov. can be easily distinguished from *G. clavatus* and *G. lepidus* by the clavate proboscis (*vs* proboscis nearly cylindrical in *G. clavatus* and *G. lepidus*), distinctly longer trunk (male 46.0–65.5 mm, female 55.3–110.5 mm in the new species *vs* male and female not over 30.0 mm in both *G. clavatus* and *G. lepidus*). Moreover, the lemnisci of *G. clavatus* are distinctly shorter than that of *G. fistularius* sp. nov. (lemnisci 1.5–2.0 times the length of the

Table 3. Morphometric comparisons of *Gorgorhynchus* spp. *Indicated these values calculated by the present authors based on the previous descriptions.

Species	*G. fistularius* sp. nov.	*G. celebensis* (Yamaguti, 1954)	*G. clavatus* Van Cleave, 1940	*G. lepidus* Van Cleave, 1940	*G. medius* (Linton, 1907)	*G. nemipteri* Parukhin, 1973	*G. occultus* Smales, Barton & Chisholm, 2019
Trunk size (mm)							
Male	46.0–65.5	6.25	—	7–10	42.0	18.5–25.0	45.0–50.0
Female	55.3–110.5	—	26.0		54.0	28.0–35.0	30.0–45.0
Proboscis length (mm)							
Male	0.55–0.75	0.52–0.60	—	0.80–1.60	1.40	0.90–1.00	0.57–0.74
Female	0.65–0.80	—	1.25–1.50		—	1.00–1.20	0.54–0.64
Proboscis shape	clavate	clavate	cylindrical	cylindrical	linear/fusiform	clavate	clavate
Number of hook rows in proboscis	20–22	20	20	20	22	24	18–20
Number of hooks per row	10–12	11–12	13–15	14–16	20	12–13	8–9
Field of trunk spines	1	2	1	1	1	1	1
Length of lemnisci / proboscis receptacle	*3.0–4.0 times	—	1.5–2.0 times	3.0 times	*1.8 times	*3.5–5.0 times	4.5 times
Host	*Fistularia petimba*	*Caranx* sp.; *Synagris* sp.	*Paralabrax humeralis*	*Cratinus agassizii*	*Mycteroperca apua*	*Nemipterus smithi*; *Trichiurus lepturus*; *Epinephelus ascolatus*	*Sutorectus tentaculatus*
Location	China	Indonesia	Ecuador	Ecuador	Britain	Oman	Australia
Reference	Present study	Yamaguti (1954)	Van Cleave (1940)	Van Cleave (1940)	Chandler (1934)	Parukhin (1973)	Smales et al. (2019)

Species	*G. ophiocephali* Furtado & Lau, 1971	*G. polymixiae* Kovalenko, 1981	*G. robertdollfusi* Golvan, 1956	*G. satoi* (Morisita, 1937)	*G. tonkinensis* Amin & Van Ha, 2011	*G. trachinotus* Noronha, Vicente, Pinto & Fábio, 1986	*G. valiyathurae* (Nadakal, John & Jacob, 1990)
Trunk size (mm)							
Male	—	—	—	4.73	5.87	8.73	78.0–112
Female	—	—	12.0	4.67–4.90	—	8.36	81.0–138
Proboscis length (mm)							
Male	—	—	—	0.58	0.57	1.00	1.01–1.06
Female	—	—	0.60	0.62–0.64	—	—	—
Proboscis shape	—	—	oval	clavate	cylindrical	cylindrical	clavate
Number of hook rows in the proboscis	32–36	17–18	18	24–26	22	14	10–16
Number of hooks per row	12–14	8–9	10–12	15–18	7–8	11–12	18–24
Field of trunk spines	1	1	1	1	1	1	1
Length of lemnisci / proboscis receptacle	—	2.0 times	*0.8 times	*1.5–2.0 times	*3.5 times	*1.0–1.5 times	*12.0–14.0 times
Host	—	—	*Gempylus serpens*	*Lateolabrax japonicus*; *Glossogobius giuris*; *Eleotris pisonis*	*Decapterus kurroides*	*Trachinotus goodei*	*Caranx melanopygus*; *C. malabaricus*; *C. nigripinnis*
Location	Malaysia	Philippine	Mauritania	China	Vietnam	Brazil	India
Reference	Amin and Van Ha (2011)	Kovalenko (1981)	Golvan (1956)	Leotta et al. (1982)	Amin and Van Ha (2011)	Noronha et al. (1986)	Nadakal et al. (1990)

proboscis receptacle in *G. clavatus vs* lemnisci 3.0–4.0 times the length of proboscis receptacle in the new species). *Gorgorhynchus lepidus* has 14–16 proboscis hooks per row, much more than that of *G. fistularius* sp. nov. (*vs* only 10–12 proboscis hooks per row).

In *Gorgorhynchus*, only *G. satoi* (Morisita, 1937) has been reported in China (Morisita 1937; Yamaguti 1963; Wang and Wang 1988). Morisita (1937) first described *Neoacanthorhynchus satoi* from *Lateolabrax japonicus* (Perciformes, Oligoridae) in the Yellow Sea (off Qingdao, China). Yamaguti (1963) transferred this species into *Gorgorhynchus*. *Gorgorhynchus satoi* also has the clavate proboscis, that is similar to *G. fistularius* sp. nov. However, the proboscis of *G. satoi* with 24–26 rows of 15–18 hooks each, which is different from that of the new species (*vs* proboscis with 20–22 rows of 10–12 hooks each in *G. fistularius* sp. nov.).

Recent studies have proved the significance of some molecular markers (*i.e.*, 28S, ITS, *cox*1, *cox*2) for species identification of acanthocephalans, especially for

revealing cryptic species and delimiting phenotypic variation (Li et al. 2017, 2019; Zhao et al. 2025; Wang et al. 2025). Additionally, the 18S rRNA gene with slow evolutionary rate can provide valuable reference for investigating of the phylogenetic relationships of higher taxa within the Acanthocephala (García-Varela and Nadler 2005). However, the current genetic data base for the isthmosacanthid acanthocephalans is still insufficient. In the genus *Gorgorhynchus*, only *G. medius*, *G. lepidus* and *Gorgorhynchus* sp. have been sequenced for the 18S, 28S and *cox*1 data (Vidal-Martínez et al. 2019; Martínez-Aquino et al. 2023). Consequently, we presented the genetic data of 18S, 28S, ITS, *cox*1 and *cox*2 for *G. fistularius* sp. nov. in this study. Genetic analysis showed no nucleotide polymorphisms among different individuals of *G. fistularius* sp. nov. in both nuclear (18S, 28S and ITS) and mitochondrial (*cox*1 and *cox*2) sequences. Very low interspecific nucleotide divergence was detected in 18S (0.24%) and 28S (1.04%) regions between *G. fistularius* sp. nov. and *G. medius*. In contrast, high interspecific nucleotide variation was found in *cox*1 (17.4–18.0%) between the new species and its congeners. This study also provided the ITS and *cox*2 data of *Gorgorhynchus* for the first time, which are the powerful and practical genetic markers for DNA taxonomy of acanthocephalans. The genetic data presented here represent an important advance in the molecular identification of *Gorgorhynchus* spp.

Characterization of the complete mitogenome (Figs 4–7, Table 4, 5)

The complete mitogenome of *G. fistularius* sp. nov. is 14,409 bp in length, and includes 36 genes, containing 12 PCGs (*cox1–3*, *nad1–6*, *nad4L*, *cytb* and *atp6*; missing *atp8*), 22 tRNA genes and 2 ribosomal RNAs (*rrnL* is 910 bp in length, located between *trnY* and *trnL1*; *rrnS* is 562 bp in length, located between *trnM* and *trnF*), plus 2 non-coding regions (*LNCR* is 908 bp, located between *trnW* and *trnV*; *SNCR* is 290 bp, located between *trnI* and *trnM*) (Fig. 4, Table 4). All genes are encoded on the same strand in the same direction. The overall A+T content in the mitogenome of *G. fistularius* sp. nov. is 68.1%, displaying a strong nucleotide compositional bias toward A + T. The base composition and nucleotide skewness of mitogenome of *G. fistularius* sp. nov. are provided in Table 5.

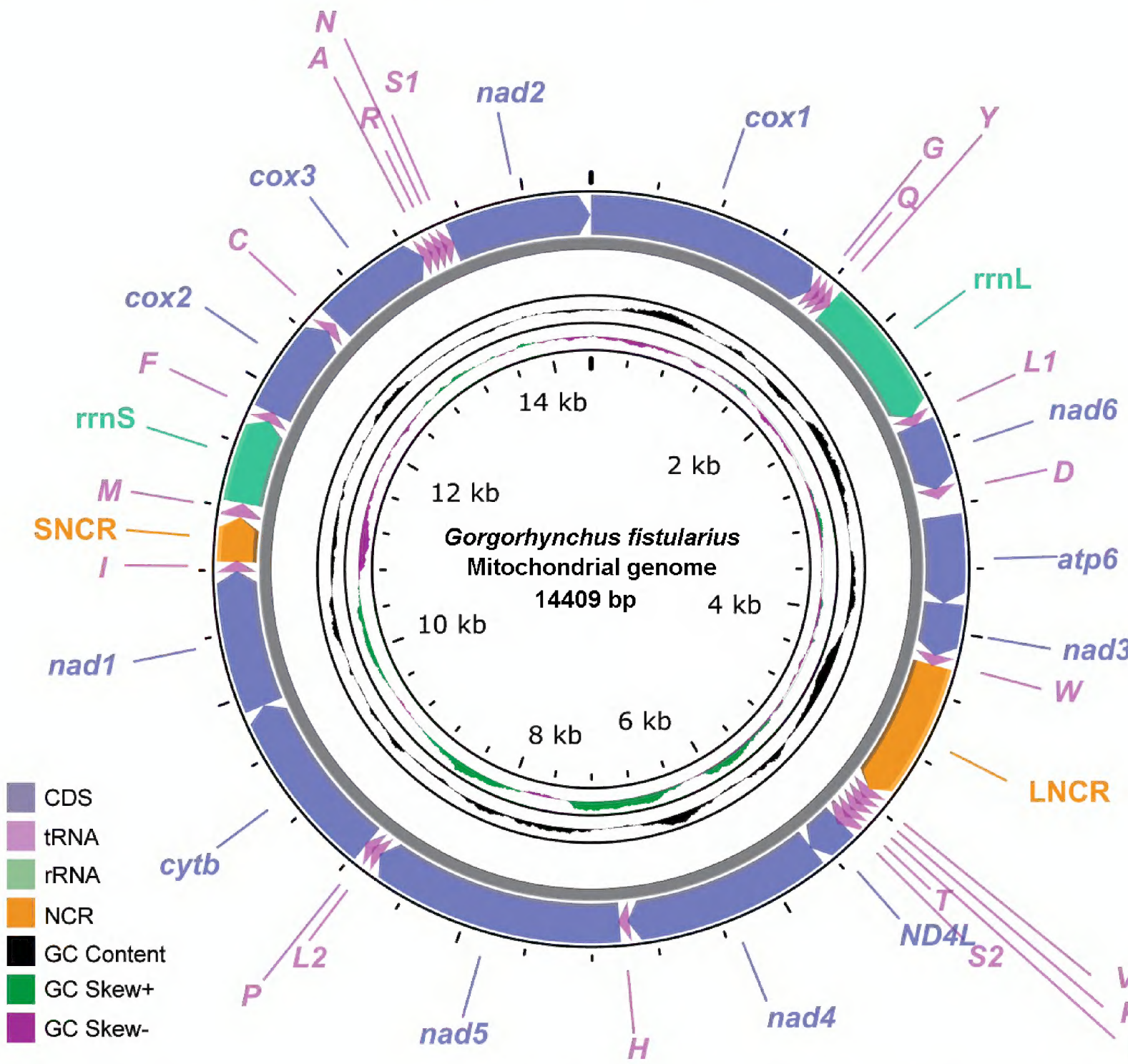

Figure 4. Gene map of mitochondrial genome of *Gorgorhynchus fistularius* sp. nov. All 22 tRNA genes are nominated by the one-letter code with numbers differentiating each of the two tRNAs, serine and leucine. All genes are transcribed in the clockwise direction on the same strand. The outermost circle shows the GC content and the innermost circle shows the GC skew.

Table 4. Annotations and gene organization of the mitogenome of *Gorgorhynchus fistularius* sp. nov. The positive number in the "Gap or overlap" column indicates the length of intergenic sequence, and the negative number indicates the length (absolute number) that adjacent genes overlap (negative sign).

Gene	Type	Start	End	Length (bp)	Start Codon	Stop Codon	Anticodon	Gap or overlap
cox1	CDS	1	1533	1533	GTG	TAG		-2
trnG	tRNA	1532	1584	53			UCC	-7
trnQ	tRNA	1578	1632	55			UUG	-5
trnY	tRNA	1628	1680	53			GUA	0
rrnL	rRNA	1681	2590	910				0
trnL1	tRNA	2591	2642	52			UAG	0
nad6	CDS	2643	3084	442	GTG	T		0
trnD	tRNA	3085	3136	52			UGC	122
atp6	CDS	3259	3825	567	TTG	TAG		-1
nad3	CDS	3825	4170	346	GTG	T		0
trnW	tRNA	4171	4230	60			UCA	908
LNCR	LNCR	4231	5138	908				
trnV	tRNA	5139	5199	61			UAC	1
trnK	tRNA	5201	5252	52			UUU	1
trnE	tRNA	5254	5305	52			UUC	0
trnT	tRNA	5306	5372	67			UGU	-25
trnS2	tRNA	5348	5446	99			UGA	-26
nad4L	CDS	5421	5678	258	ATG	TAA		-7
nad4	CDS	5672	6970	1299	TTG	TAA		-1
trnH	tRNA	6970	7021	52			GUG	0
nad5	CDS	7022	8668	1647	GTG	TAG		-1
trnL2	tRNA	8668	8720	53			UAA	1
trnP	tRNA	8722	8774	53			UGG	0
ctyb	CDS	8775	9902	1128	GTG	TAG		0
nad1	CDS	9903	10796	894	TTG	TAA		1
trnI	tRNA	10798	10854	57			GAU	0
SNCR	SNCR	10855	11144	290				0
trnM	tRNA	11145	11235	91			CAU	0
rrnS	rRNA	11236	11797	562				0
trnF	tRNA	11798	11850	53			GAA	0
cox2	CDS	11851	12498	648	ATG	TAG		
trnC	tRNA	12497	12549	53			GCA	21
cox3	CDS	12571	13281	711	GTG	TAA		-2
trnA	tRNA	13280	13334	55			UGC	0
trnR	tRNA	13335	13392	58			ACG	-1
trnN	tRNA	13392	13434	43			GUU	0
trnS1	tRNA	13435	13491	57			ACU	0
nad2	CDS	13492	14406	915	ATG	TAA		3

The 12 PCGs of *G. fistularius* sp. nov. mitogenome have 10,388 bp (excluding termination codons), and encode 3,462 amino acids. The size of each of 12 PCGs are from 258 bp (*nad4L*) to 1,647 bp (*nad5*) (Fig. 4, Table 4). Among the 12 PCGs of *G. fistularius* sp. nov., six genes (*cox1*, *cox3*, *nad3*, *nad5*, *nad6* and *cytb*) use GTG as the start codon, while three genes (*nad1*, *nad4* and *atp6*) use TTG, and the remaining three genes (*cox2*, *nad2* and *nad4L*) use ATG as the start codon, respectively. Five genes (*cox1*, *cox2*, *nad5*, *cytb* and *atp6*) use TAG as the termination codon, and five genes (*cox3*, *nad1*, *nad2*, *nad4* and *nad4L*) use TAA as the termination codon, respectively. The remaining two genes (*nad3* and *nad6*) are inferred to terminate with incomplete stop codon T (Table 4). The component and usages of codons in the mitogenome of *G. fistularius* sp. nov. are shown in Fig. 5. The lengths of 22 tRNAs and their anticodon secondary structures are provided in Fig. 6 and Table 4. In the mitogenome of *G. fistularius* sp. nov., the order of 36 gene arrangements is identical to species of the Polymorphidae (ex. *Southwellina hispida*) (Fig. 7).

Phylogenetic analyses

Phylogenetic results based on the concatenated amino acid sequences of 12 protein-coding genes (PCGs) using the ML and BI methods, are nearly identical in the topology (Fig. 8), which showed the Acanthocephala comprises three major monophyletic clades. Clade I contains species of the orders Echinorhynchida and Polymorphida, representing the class Palaeacanthocephala. In Polymorphida,

Figure 5. Relative synonymous codon usage (RSCU) of *Gorgorhynchus fistularius* sp. nov. The codon families (in alphabetical order) are labelled on the x-axis. Values on the top of each bar represent amino acid usage in percentage.

Table 5. Base composition and nucleotide skewness of mitogenome of *Gorgorhynchus fistularius* sp. nov.

Location	A%	T%	C%	G%	AT%	AT-skew	GC-skew	Total (bp)
Whole mitochondrial genome	25.5	42.56	8.58	23.11	68.06	-0.25	0.46	14409
Protein coding genes (PCGs)	22.88	44.05	8.33	24.74	66.93	-0.32	0.50	10388
1st codon	25.4	34.84	8.86	30.89	60.25	-0.16	0.55	3464
2nd codon	14.64	50.06	11.50	23.80	64.70	-0.55	0.35	3462
3rd codon	28.6	47.26	4.62	19.53	75.85	-0.25	0.62	3462
tRNAs	28.88	38.95	9.99	22.17	67.83	-0.15	0.38	1281
rRNAs	33.29	36.01	10.53	20.18	69.29	-0.04	0.31	1472
rrnS	33.99	35.41	10.14	20.46	69.40	-0.02	0.34	562
rrnL	32.86	36.37	10.77	20.00	69.23	-0.05	0.30	910
Long non-coding region (LNCR)	33.81	44.82	6.28	15.09	78.63	-0.14	0.41	908
Short non-coding region (SNCR)	41.98	33.11	12.63	12.29	75.09	0.12	-0.01	290

G. fistularius sp. nov. formed a distinct lineage, representing the family Isthmosacanthidae, which showed a sister relationship with the Centrorhynchidae + Polymorphidae.

Clade II includes the representatives of the orders Gyracanthocephala and Neoechinorhynchida of the class Eoacanthocephala, together with the class Polyacanthocephala (*Polyacanthorhynchus caballeroi*). Clade III comprises species of the orders Oligacanthorhynchida and Moniliformida, representing the class Archiacanthocephala.

Discussion

The present knowledge of the mitogenomes for Acanthocephala remains insufficient, and there are no data on the mitogenomes of representatives for approximately 20 families, including the Isthmosacanthidae. The mitogenome of *G. fistularius* sp. nov. with 14,409 bp in length, represents the first mitogenomic data for the genus *Gorgorhynchus* and also for the family Isthmosacanthidae. The mitogenome of *G. fistularius* sp. nov. contains 36 genes (12 PCGs, 22 tRNAs and 2 rRNAs), lacking *atp*8, which is common in Acanthocephala (Gazi et al. 2016; Xie et al. 2025a, 2025b; Zhao et al. 2025). To date, only the mitogenome of *Leptorhynchoides thecatus* has been reported to have putative *atp*8 gene (Steinauer et al. 2005). The overall A+T content in the mitogenome of *G. fistularius* sp. nov. is 68.1%, which is distinctly higher than that of the other mitogenomes of the order Polymorphida reported so far (54.5–64.4%) (see Table 2 for details). Among all the known mitogenomes of acanthocephalans, only *Brentisentis yangtzensis* (68.3%) and *Leptorhynchoides thecatus*

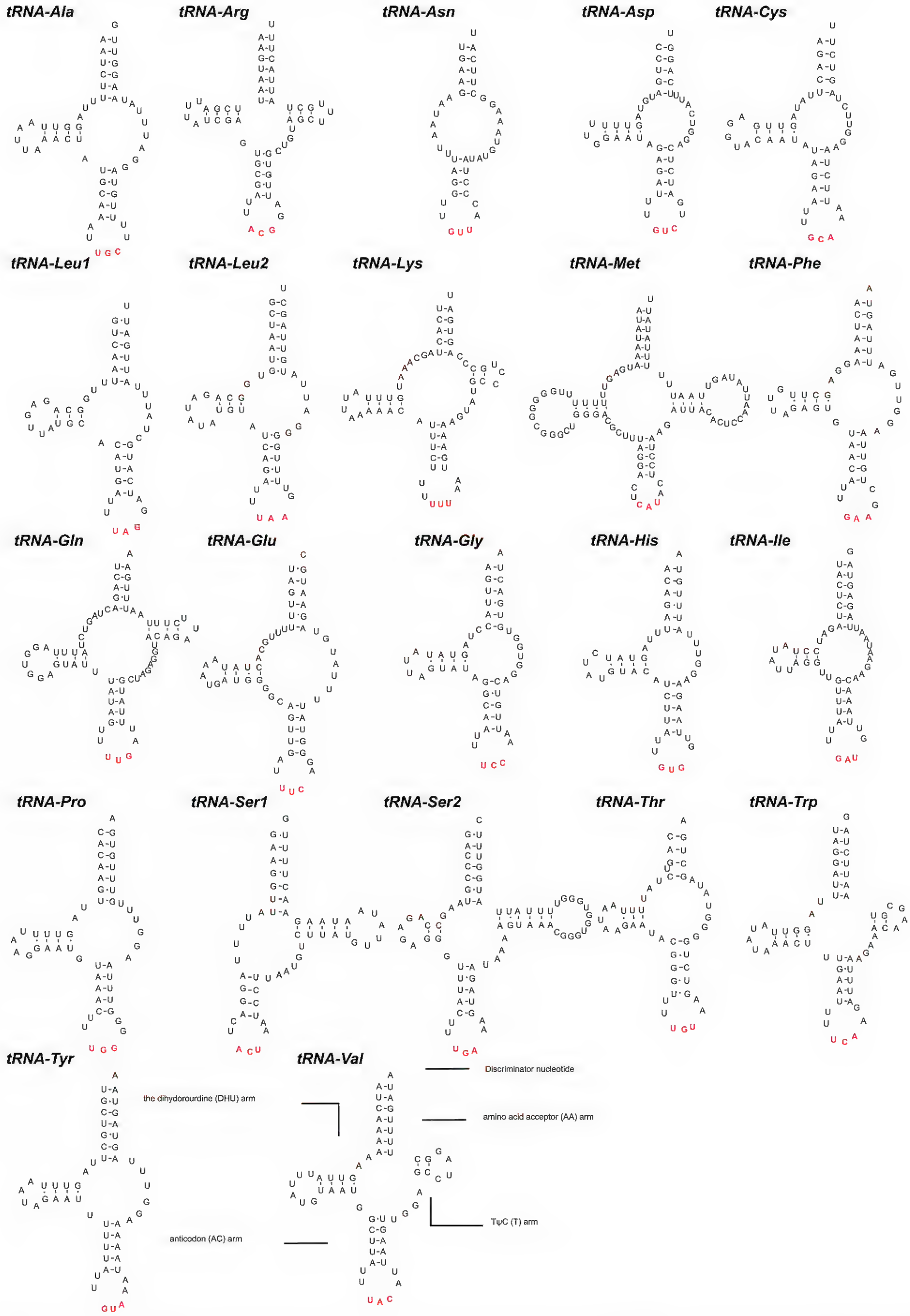

Figure 6. Inferred secondary structures of 22 tRNAs in the mitogenome of *Gorgorhynchus fistularius* sp. nov. Lines between bases indicate Watson–Crick bonds, dots indicate GU bonds and bases in red represent anticodons. tRNA, Transfer RNA.

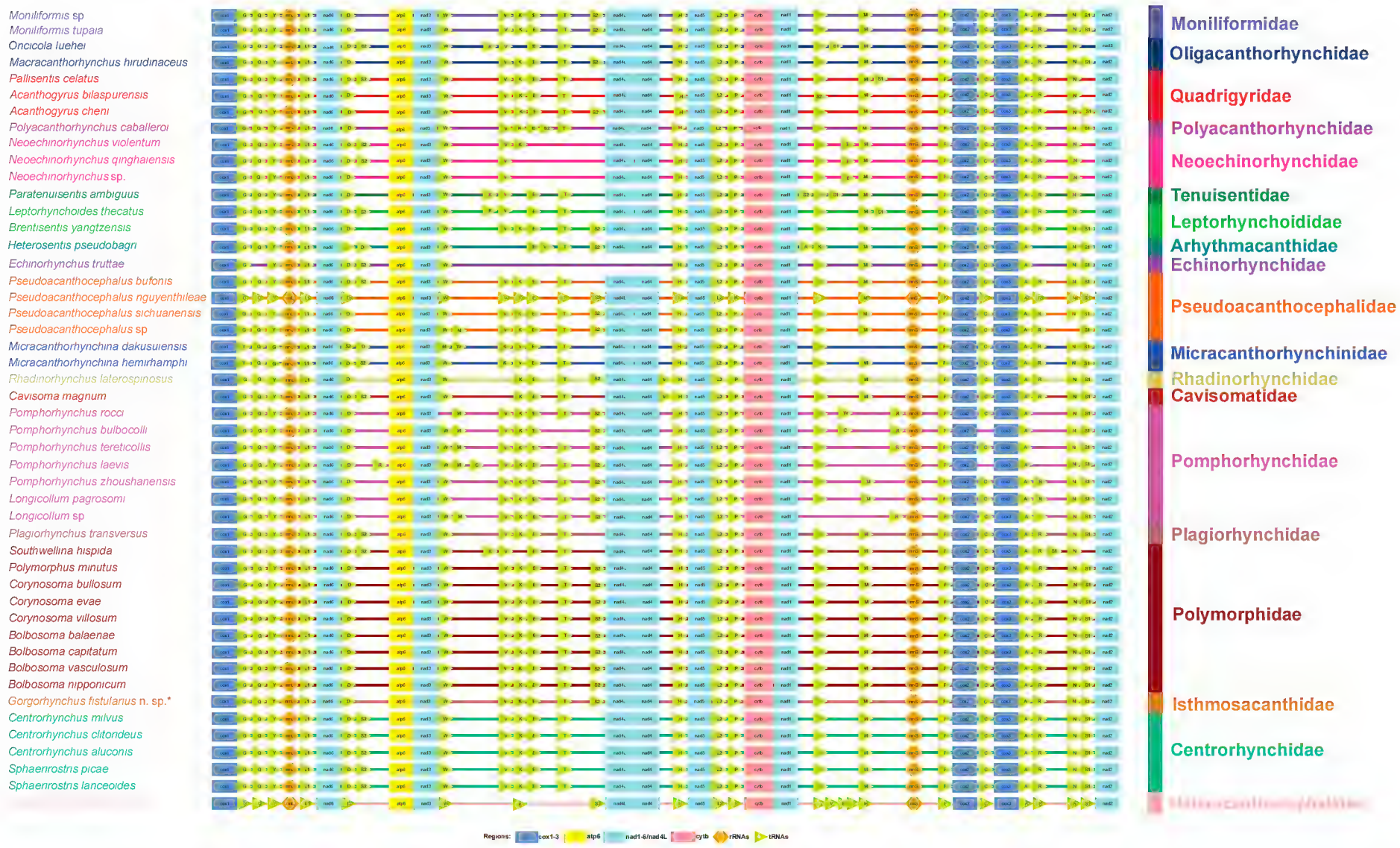

Figure 7. Comparison of the linearized mitochondrial genome arrangement for acanthocephalans species. All genes are transcribed in the same direction from left to right. The tRNAs are labelled by a single-letter code for the corresponding amino acid. *Gorgorhynchus fistularius* sp. nov. is indicated using an asterisk (*).

(71.4%) both belonging to the family Leptorhynchoididae (Song et al. 2019; Steinauer et al. 2005), have the A+T content higher than *G. fistularius* sp. nov. The high A-T content in mitogenomes of acanthocephalan seems to be driven by mutational bias, energy efficiency and evolutionary origin, rather than functional adaptive mechanisms. Additionally, comparative mitochondrial genomic analysis revealed that the composition and gene rearrangement of the mitogenome of *G. fistularius* sp. nov. are identical to the current known mitogenomes of polymorphid species except for *Southwellina hispida*, which has two tRNA gene (*trnK* and *trnS2*) rearrangement (Gazi et al. 2015; Sarwar et al. 2021; Li et al. 2024; Xie et al. 2025a; García-Gallego et al. 2025).

The family Isthmosacanthidae was erected by Smales (2012) and initially assigned to the non-monophyletic order Echinorhynchida (García-Varela and Nadler 2005; Verweyen et al. 2011). Huston et al. (2020) established the family Pyriprobosicidae and suggested to transfer the Isthmosacanthidae and Pyriprobosicidae into the order Polymorphida based on the phylogeny of 18S + 28S data, which indicated that the Isthmosacanthidae is a sister to Centrorhynchidae + Pyriprobosicidae. The subsequent molecular phylogenetic results based on the single (18S / 28S / *cox*1) or some concatenated genetic markers (18S + 28S / 18S + 28S + *cox*1) all supported the change of the systematic position of the Isthmosacanthidae, but the phylogenetic relationships between the Isthmosacanthidae and the other families within Polymorphida are inconsistent (Kita et al. 2023, 2024; García-Varela et al. 2024).

The present mitogenomic phylogenetic results based on the concatenated amino acid sequences of 12 PCGs, also supported that the Isthmosacanthidae represented a separate family, and revealed that the Isthmosacanthidae is a sister to Centrorhynchidae + Polymorphidae in the order Polymorphida, which are different from previous pylogenies based on the single (18S / 28S / *cox*1) or some concatenated genetic markers (18S + 28S / 18S + 28S + *cox*1) (García-Varela and Nadler 2005; García-Varela and Andrade-Gómez 2021; Huston et al. 2020; Kita et al. 2023, 2024; García-Varela et al. 2024). However, our mitogenomic phylogeny included only single species of the genus *Gorgorhynchus*, and also lacked a representative of the Pyriprobosicidae. Consequently, the interfamilial relationships of these families Centrorhynchidae, Isthmosacanthidae, Plagiorhynchidae, Pyriprobosicidae, and Polymorphidae in the order Polymorphida remain unsolved. A more rigorous mitogenomic phylogenetic study that includes broader representatives of the order Polymorphida, especially species of the families Isthmosacanthidae, Plagiorhynchidae and Pyriprobosicidae, is needed to further solve the deep phylogenetic relationships of these families in the order Polymorphida.

Conclusions

Gorgorhynchus fistularius sp. nov. (Polymorphida, Isthmosacanthidae) is described based on specimens collected from the red cornetfish *Fistularia petimba*

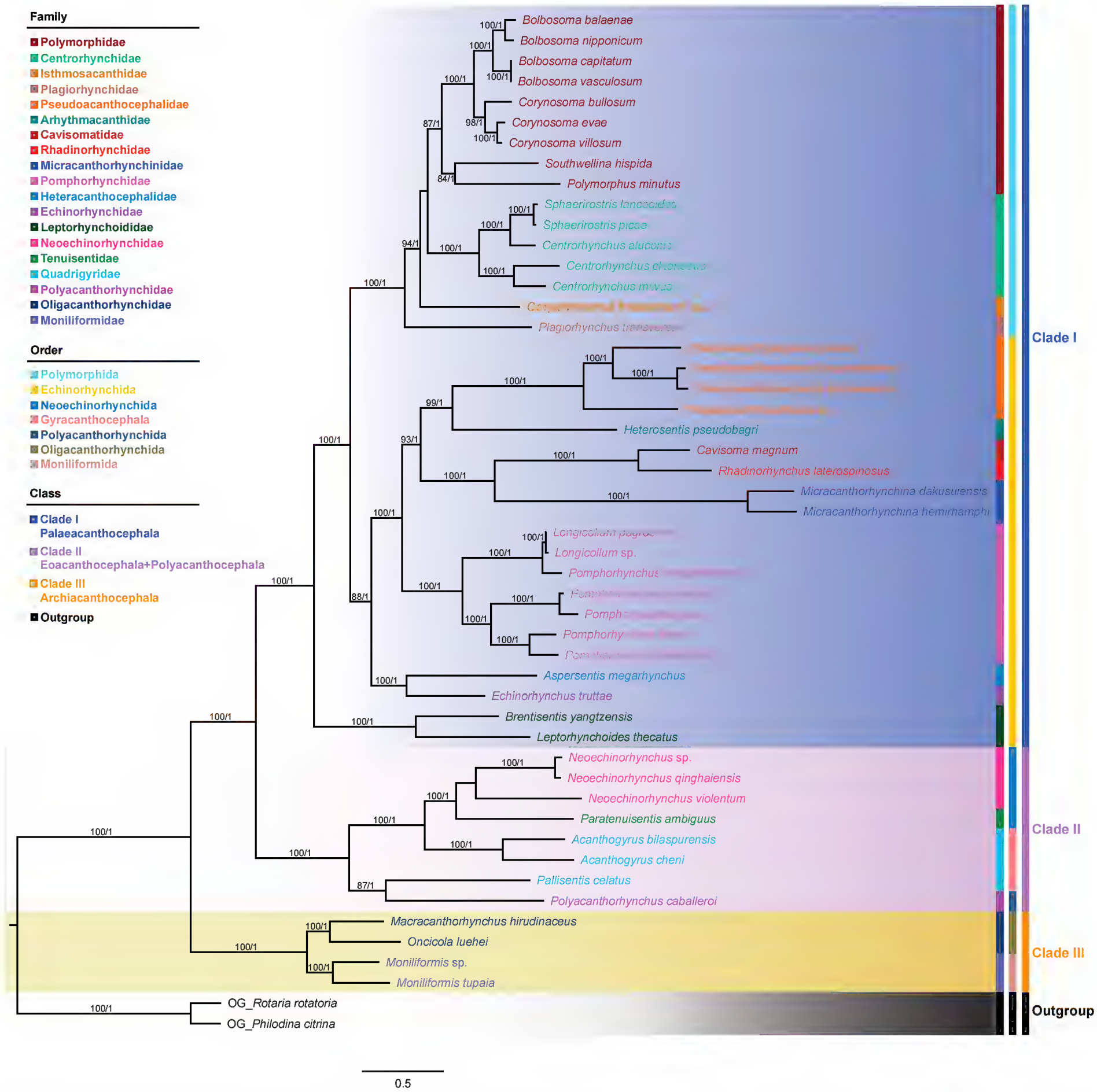

Figure 8. Phylogenetic analyses of Acanthocephala inferred from ML and BI methods based on concatenated amino acid sequences of 12 protein-coding genes (PCGs) of mitochondrial genomes. *Rotaria rotatoria* and *Philodina citrina* were treated as the out-group. Bootstrap values ≥ 70 and Bayesian posterior probabilities values ≥ 0.95 were shown in the phylogenetic trees.

Lacépède (Syngnathiformes, Fistularidae) using the integrated morphological characters and molecular data. The complete mitochondrial genome of *G. fistularius* sp. nov. with 14,409 bp in length includes 36 genes, containing 12 PCGs (missing *atp8*), 22 transfer RNA (tRNA) genes, and two ribosomal RNAs (*rrnS* and *rrnL*), plus two noncoding regions, which is the first for the genus *Gorgorhynchus* and also for the family Isthmosacanthidae. Comparative mitogenomic analysis revealed that the overall A+T content (68.1%) in the mitogenome of *G. fistularius* sp. nov. is distinctly higher than that of the other mitogenomes of the order Polymorphida reported so far (54.5–64.4%), but the composition and gene rearrangement of the mitogenome of *G. fistularius* sp. nov. are identical to the current known mitogenomes of polymorphid species except for *Southwellina hispida*. Mitogenomic phylogenies supported the Isthmosacanthidae as a distinct family, and revealed that the Isthmosacanthidae is a sister to Centrorhynchidae + Polymorphidae in the order Polymorphida.

Authors' contributions. HXC and LL contributed to the study design and identification of the acanthocephalan specimens. HXC, SSW and RJY sequenced and analyzed genetic data. HXC and LL conducted the phylogenetic analyses. HXC, ZJY and LL wrote the manuscript. All authors read and approved the final manuscript.

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